MORPHOLOGY AND DEVELOPMENT OF SUNKEN TERMINAL CEPHALIUM IN *DISCOCACTUS* (CACTACEAE)

Root Gorelick
Department of Biology, School of Mathematics and Statistics, and
Institute of Interdisciplinary Studies, Carleton University, 1125 Colonel By Drive,
Ottawa, Ontario, Canada, K1S 5B6
Root.Gorelick@carleton.ca

Abstract

Growth of photosynthetic portions of *Discocactus* shoots is seemingly not suppressed by cephalium formation, as vascular traces are prominent between the vascular cylinder and the circular juncture of cephalium and juvenile growth. Neither of these morphological traits has previously been documented in the Cactaceae. I therefore provide a pair of hypotheses consistent with these morphological traits and suggest ways to test these hypotheses, although do not test them myself. One hypothesis for these morphological traits is that the shoot vascular cylinder bifurcates when the cephalium first forms, with one cylindrical 'branch' of the vascular cambium terminating in the shoot apical meristem and the other concentric cylindrical 'branch' of the vascular cambium terminating in a circular meristem at the base of the terminal cephalium. A second hypothesis is that subapical development occurs very slowly surrounding a depressed shoot apical meristem in *Discocactus*. Vegetative portions of the shoot mature sufficiently slowly that the cephalium can be well formed even while juvenile areoles and photosynthetic internodes continue to grow and develop for several years after production by the juvenile phase of the shoot apical meristem.

Key Words: Cephalium, *Coleocephalocereus*, *Discocactus*, *Espostoa*, *Melocactus*, Podostemaceae, shoot apical meristem, vascular cambium.

Several species of the family Cactaceae possess highly modified reproductive structures known as terminal cephalia. In these species, a single shoot apical meristem begins life as a normal-looking photosynthetic cactus, but eventually undergoes a juvenile/adult transition to form a non-photosynthetic apical portion of the shoot, called a terminal cephalium (the adjective 'terminal' is a misnomer and should probably be called an 'apical cephalium' because the cephalium grows indefinitely from the shoot apical meristem). The cephalium contains contiguous axillary buds that produce huge numbers of hairs, bristles and spines, each of which are highly modified leaves. Terminal cephalia occur in two different clades of cacti, Pachycereinae in the Core Cactoideae I and the Browningieae-Cereeae-Trichocereeae clade in the Core Cactoideae II (Hernández-Hernández et al. 2011) (although some botanists call the reproductive structures in Pachycereinae 'pseudocephalia'; see the discussion section regarding *Cephalocereus* Pfeiff. and see hypothesis two regarding *Pachycereus* Britton & Rose). In several taxa (*Stephanocereus leucostele* A. Berger, *Arrojadoa* Britton & Rose, and *Cephalocereus apicicephalium* E. Y. Dawson), the shoot apical meristem later reverts to producing the photosynthetic juvenile morphology, thereby forming a series of ring-like terminal cephalia. However, in *Melocactus* Link & Otto, *Discocactus* Pfeiff., and *Pachycereus militaris* (Audot) D. R. Hunt, the

conversion of the shoot apical meristem from juvenile to adult form is permanent: Once a terminal cephalium is formed, it continues to grow and produce flowers until the shoot or portion of the shoot dies (in *Pachycereus militaris* the portion of the shoot containing all of the cephalium and small part of the underlying photosynthetic tissue abscises and dies, but the remainder of the vegetative shoot below usually lives for many more years, forming new vegetative and reproductive shoots from axillary branches; Mauseth et al. 2005).

In a detailed review of anatomy of highly modified shoots in the Cactaceae, Mauseth (pp. 910, 2006) asserted that for *Melocactus*, *Discocactus*, and *Pachycereus militaris*, "The cephalium becomes longer every year, every year the juvenile portion merely becomes older – and it is the only photosynthetic tissue the plant has. Because the shoot is produced by one single SAM (shoot apical meristem) and does not branch, no new photosynthetic cortex can be added, so the ratio of photosynthetic tissue to heterotrophic tissue decreases every year." If true, this would be especially problematic for *Melocactus* and *Discocactus* because their terminal cephalia appear to completely lack chlorenchyma and stomata and because photosynthetic portions of their shoots only branch when seriously injured.

In this paper, I show an exception to the claim of no new photosynthetic growth after cephalium formation for several species of *Discocactus*. I

FIG. 1a, b. *Discocactus heptacanthus* Britton & Rose subsp. *catingicola* (Buining & Brederoo) N.P. Taylor & Zappi (synonym *D. catingicola* Buining & Brederoo) near Porto Novo, Bahia, Brazil showing new photosynthetic growth at the base of the terminal cephalium. The cephalium in Figure 1b is about four to five times the diameter of the cephalium in Figure 1a.
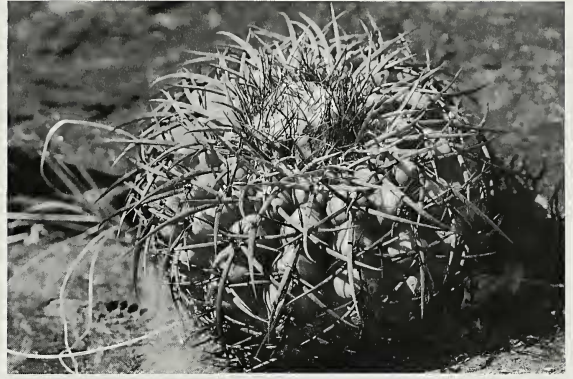

FIG. 2. *Discocactus placentiformis* (synonyms *D. latispinus* Buining & Brederoo, *D. crystallophilus* Diers & Esteves) near Monjolos, Minas Gerais, Brazil with new vegetative spines surrounding the cephalium at the 7 o'clock position.

further discuss two hypotheses to explain this observation.

Figure 1a shows a mature shoot of *Discocactus heptacanthus* Britton & Rose subsp. *catingicola* (Buining & Brederoo) N.P. Taylor & Zappi (synonym *D. catingicola* Buining & Brederoo) with a cephalium that is probably a few years old, but also with new photosynthetic tissue and cortex, including new axillary buds (areoles, with spines) arising from just below the cephalium. The brown color of the spines surrounding the base of the cephalium shows that these are probably new leaves on newly formed axillary buds. The beige colored trichomes in these axillary buds also indicate that this is new growth. Other plants of this subspecies (*D. heptacanthus* subsp. *catingicola*), with even larger cephalia, show this new growth after cephalium formation (Fig. 1b).

Buining's (1980) monograph on *Discocactus* shows two taxa growing new vegetative tissue after cephalium formation, *D. catingicola* (pp. 179) and *D. griseus* Buining & Brederoo (pp. 175), both of which are usually considered synonyms of *D. heptacanthus*. New photosyn-

thetic tissue also appears to be produced from the base of the cephalium in at least two other taxa, *D. placentiformis* K. Schum. (synonyms *D. latispinus* Buining & Brederoo, *D. crystallophilus* Diers & Esteves) and *D. bahiensis* Britton & Rose subsp. *gracilis* P.J. Braun & Esteves (Figs. 2–4).

The genus *Discocactus* was named for the accentuated disc-shaped form of the photosynthetic portion of the shoot. *Discocactus* photosynthetic stems are proportionally much wider than those of *Melocactus* or *Pachycereus militaris*. This also explains how *Discocactus* shoots grow cephalia at fairly small sizes, but large diameter photosynthetic stems are often noted in the field. Disc-shaped photosynthetic juvenile stems are ubiquitous in the genus *Discocactus*, not just in *D. heptacanthus*, *D. placentiformis,* and *D. bahiensis*. Several of the ground-hugging (virtually geophytic) members of the genus, such as *D. bahiensis* subsp. *gracilis* (Fig. 4) and *D. horstii* Buining & Brederoo would probably perish without this ability to grow new photosynthetic tissue as the older chlorenchyma gets trampled.

Widening of the photosynthetic portion of the shoot after initial cephalium formation largely debunks the notion that newly formed spines at the base of the cephalium are the product of indeterminate growth of vegetative (juvenile) areoles. For example, *Espostoa blossfeldiorum* (Werdermann) Buxbaum grows a basal skirt of spines for many years after seedling germination. Cephalia too can have indeterminate growth of areoles, as seen in *Espostoa lanata* (Kunth) Britton & Rose and *Coleocephalocereus goebelianus* (Vaupel) Buining, which can both flower and grow axillary branches from areoles that are several years old (Gorelick and Machado 2012; Gorelick 2014). *Discocactus* species, however, do more than grow new nodes (areoles) below the cephalium. They also grow new internodes,
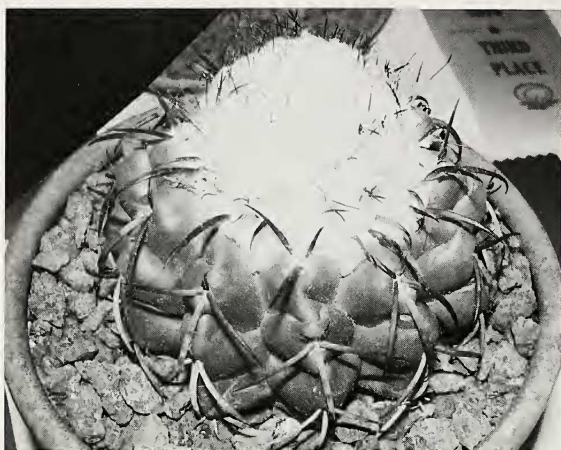
apparently with new chlorenchyma, and grow a substantially wider shoot.

A radial section of a mature cultivated specimen of *Discocactus zehntneri* Britton & Rose subsp. *araneispinus* (Buining & Brederoo) P.J. Braun showed a remarkably sunken cephalium and vascular traces arising from the vascular cylinder to the epidermal juncture between juvenile growth and cephalium (Fig. 5). This is consistent with new photosynthetic growth and new juvenile areoles formed after the cephalium arose, but in two very different possible ways.

Hypothesis 1: Bifurcation of Vascular Cambium Forming Concentric Vascular Cambia

I hypothesize bifurcation of the vascular cambium to form a second concentric cambium that terminates as a circular meristem at the base of the cephalium. Such a circular meristem would cause the photosynthetic base of the shoot to grow wider over time, after cephalium formation. This circular meristem would make *Discocactus* photosynthetic stems proportionally much wider than those of *Melocactus* and *Pachycereus militaris*. This would also explain how *Discocactus* shoots grow cephalia at fairly small sizes, but large diameter photosynthetic shoots are often noted in the field. Given how short terminal cephalia are in all species of *Discocactus*, especially compared with the closely related genus *Melocactus*, a circular meristem in *Discocactus* would probably only contribute new tissue to the photosynthetic (juvenile) portion of the shoot, while supplying little or no new tissue to the cephalium.

Fig. 4. *Discocactus bahiensis* subsp. *gracilis,* near San Rafael, Bahia, Brazil with new vegetative spines surrounding the cephalium near the 12 o'clock position.

Assuming this first hypothesis, the vascular cambium bifurcated from the primary vascular cambium at around the time the cephalium first formed, with one trace of the vascular cylinder (in radial section) extending to the shoot apical meristem and the other trace extending to the junction of the cephalium and vegetative tissue. Because the terminal end of this meristem is circular (Fig. 5e), not a point (as with the shoot apical meristem), tissues derived from this circular meristem would not form a closed vascular cylinder, but rather an open funnel-shaped structure. This can be easily envisioned by rotating the vascular traces to the cephalium about a vertical axis going through the center of the pith, with the widest part of the conical frustum being the circular meristem (Fig. 5e). This could not form a closed vascular cylinder because, if it did, the tissues would completely enclose the cephalium, precluding pollinators and seed dispersers from reaching the cephalium.

The only situation possibly analogous with what I report here in *Discocactus* may occur in the aquatic family Podostemaceae, which have bizarre morphology (Eckardt and Baum 2010). For instance, *Indotristicha ramosissima* (Wight) P. Royen plants have a cup-like structure composed of parts that may be stems and/or leaves surrounding the terminal inflorescences (Rutishauser and Huber 1991) (it is not obvious what constitutes stems or leaves in the Podostemaceae). Morphologies are often unusual in submerged aquatic angiosperms, at least when compared with their terrestrial relatives.

Succulent plants are well known for adding extra layers of mitotically dividing cambial cells (Robert et al. 2011), some of which are unifacial, even including reverse cambia (Terrazas et al. 2011; Gorelick in press). But with these other taxa, concentric cambia arise from ground tissue (usually cortex), not from bifurcation of existing cambia. Making this first hypothesis less likely,
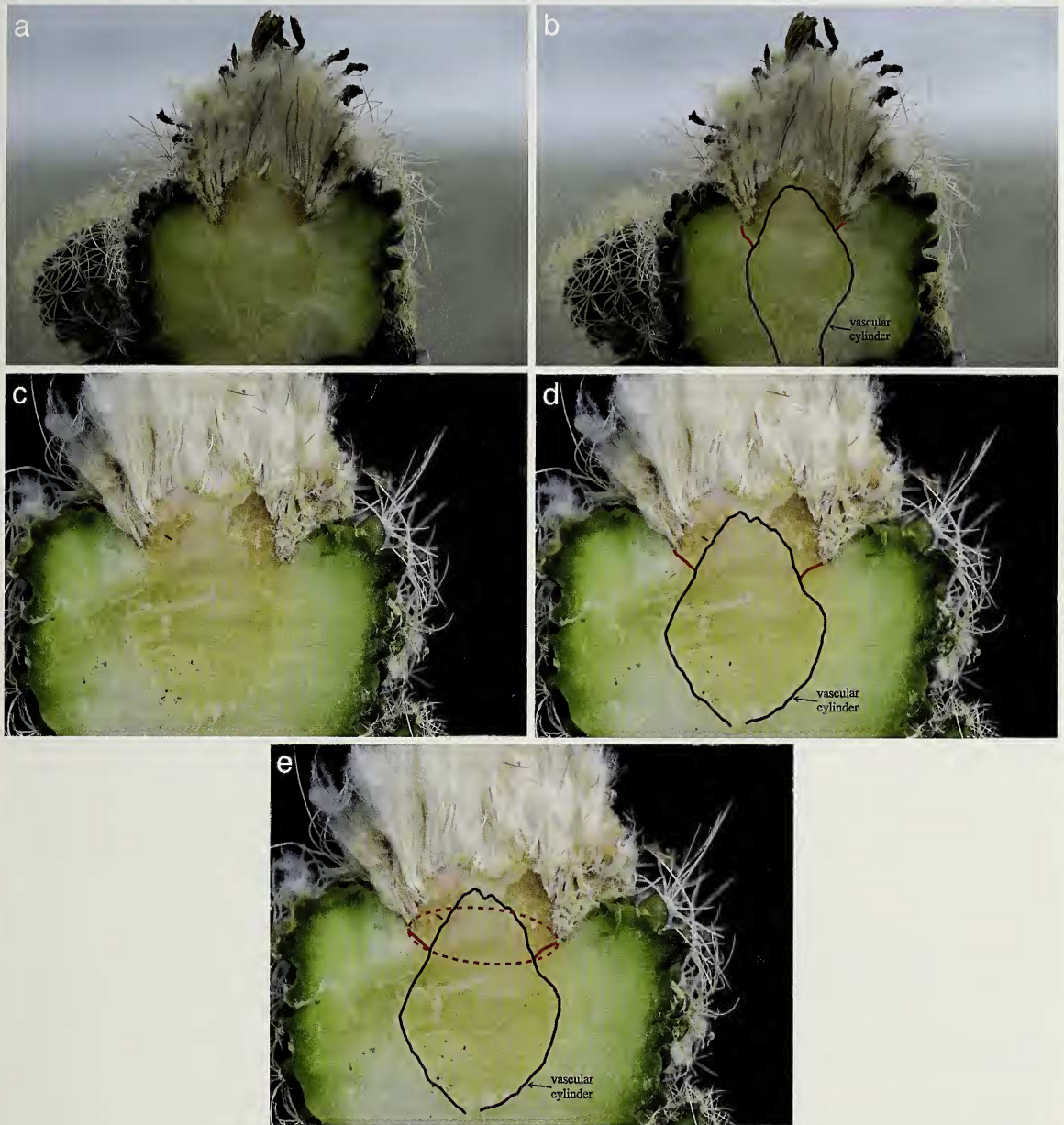
FIG. 5.   Radial section of *Discocactus zehntneri* subsp. *araneispinus* in cultivation (~10 cm diameter). 5a. One section. 5b. The same section as Fig. 5a, but with lines drawn over vascular cylinder (black) and vascular traces to the cephalium (red). 5c. Facing section. 5d. The same facing section as Fig. 5c, but with lines drawn over vascular cylinder (black) and vascular traces to the cephalium (red). 5e. If a circular meristem exists at the base of the cephalium (hypothesis 1), then that meristem would be depicted by the dotted red circle.

concentric vascular cambia have never been documented in the Cactaceae.

HYPOTHESIS 2: SLOW DEVELOPMENT OF JUVENILE AXILLARY BUDS FROM DEPRESSED SHOOT APICAL MERISTEM EVEN AFTER CEPHALIUM FORMATION

The second hypothesis is that axillary buds in the juvenile (photosynthetic) stage can take several years to fully develop. The shoot apical meristem may produce nascent juvenile-stage axillary buds and photosynthetic internodes before initial cephalium formation, but these juvenile-stage axillary buds and photosynthetic internodes may not fully develop until long after the cephalium has formed.

Discocactus is typical of the Cactaceae, especially the subfamily Cactoideae, in having a depressed shoot apical meristem, one that lies vertically below tissues that have recently developed from

it. The resulting sunken apex is thought to protect mitotically actively dividing cells from the exigencies of desert life. However, if juvenile-stage development occurs as slowly as hypothesized above, then new development of areoles and photosynthetic internodes will look as though a circular meristem has developed at the base of the cephalium. Mature and almost mature areoles (axillary buds) occupy the rim of a crater that surrounds the sunken shoot apical meristem. Slowly developing juvenile tissues exit between this rim and the shoot apical meristem. However, with this hypothesis, development of reproductive tissue in the cephalium – which arises from the same shoot apical meristem – is faster than that of later developing portions of the juvenile tissues. The cephalium and shoot apical meristem eventually overtop the slowly developing late-formed juvenile tissues. This would explain the sunken look of the lateral edges of the cephalium in radial section (Fig. 6). Mauseth (personal communication; 20 August 2013) analogizes this to formation of the caldera of a strato-volcano, such as Mount St. Helens. Inside the main caldera, subsequent magma domes can form, which can and often do overtop the rim of the caldera.

The deeply sunken lateral edges of the cephalium (Fig. 5) seem to be unique to *Discocactus*. While the phenomenon is not obvious from a casual look at a plant, but only visible with sectioning the shoot, a sunken cephalium has never been noted in radial sections of *Melocactus* nor *Pachycereus* (*Backebergia*) *militaris* (although I would say that *Pachycereus militaris* has a pseudocephalium because reproductive parts of its shoot contain stomata and parenchyma, but lack a narrow cork-laden cortex). I have never seen nor made radial sections of *Arrojadoa* nor *Stephanocereus leucostele* to see whether their terminal cephalia are sunken.

This hypothesis of slow development of late-forming juvenile (photosynthetic) tissues is also consistent with the prominent vascular trace in Figure 5 from the vascular cylinder to the epidermal juncture between juvenile tissue and cephalium (red lines in Fig. 5b, d). Especially while the cephalium is young, this juncture should be densely packed with undeveloped axillary buds. It may not even be obvious without detailed microscope examination what constitutes individual axillary buds in this slowly developing annular mass. Each axillary bud is a short shoot and therefore will have a vascular trace going to it. A sufficiently dense mass of such axillary buds should have what appears to be a dense mass of vascular traces going to them, which may look like a single large vascular trace in the radial section (Fig. 5). These nascent developing axillary buds form a circular ring around the shoot apical meristem and cephalium. Hence a cross-section of the same shoot (which

unfortunately I did not make) might show what looks like a circle of vascular traces, i.e., another vascular cylinder.

If this hypothesis of slow development of late-forming juvenile tissues is true, growth of new photosynthetic tissue should only occur for a fixed number of years after cephalium formation. While cephalium formation may start when the shoot is roughly spherical and end with the photosynthetic portion of the shoot that is substantially wider than tall, this growth can only occur for a determinate number of years. Furthermore, there will be fewer juvenile axillary buds each year in a cephalium-bearing plant, meaning fewer vascular traces to the epidermal juncture between juvenile and cephalium portions of the shoot. Thus, the apparent singular vascular trace to this juncture (red lines in Fig. 5b, d) should become less visible over time, as the photosynthetic portion of the shoot becomes wider and more disc-shaped.

This second hypothesis can be summarized as a heterochronic shift in development of the portion of *Discocactus* shoots that were epidermal mitotic products of the shoot apical meristem prior to cephalium formation, at which time these juvenile (vegetative) tissues develop slowly. Once a shoot transitions from juvenile to reproductive (cephalium) phases, epidermal mitotic products of the shoot apical meristem return to developing at a normal pace, as was found in younger juvenile stems in *Discocactus*. In other words, early juvenile (vegetative) tissues develop quickly, late juvenile (vegetative) tissues develop slowly, and reproductive (cephalium) tissues develop quickly.

DISCUSSION

Although *Discocactus* cephalia have sunken margins, this sunken nature does not appear to be homologous to the sunken lateral cephalia of *Espostoa* Britton & Rose, *Coleocephalocereus* Backeberg, or other cacti with true lateral cephalia. Lateral pseudocephalia, as in *Cephalocereus senilis* Pfeiff., *C. columna-trajani* (Karw. ex Pfeiff.) P.V. Heath, and *Micranthocereus streckeri* Van Heek & Van Criek., are not sunken (Vázquez-Sánchez et al. 2005, 2007; Gorelick 2013). True lateral cephalia are sunken in a cleft within vegetative (photosynthetic) tissue, but that cleft is relatively flat (see Fig. 7 in Gorelick 2013). By contrast, *Discocactus* cephalia have margins that are substantially depressed into the vegetative tissue. In radial sections of *Discocactus*, the boundary between vegetative and reproductive tissue is "W"-shaped, whereas in cross sections of lateral cephalia, the boundary between vegetative and reproductive tissues is "U"-shaped (Gorelick 2013). Developmentally the clefts of lateral cephalia are different from clefts of terminal (apical) cephalia of *Discocactus* insofar as they

grow in horizontal versus vertical orientations, respectively.

I cannot yet discern which of the above two hypotheses explains the peculiar morphology of *Discocactus* cephalia, with their sunken margins, nor can we discern whether all *Discocactus* species display this morphology, which is very different from that of *Melocactus*. Drastic heterochronic shifts (hypothesis 2) are more likely than concentric vascular cambia produced by a branching cambium (hypothesis 1), but neither hypothesis has been tested. Some tests of the two hypotheses should include the following. First, *Discocactus* development should be monitored over many years to determine whether new vegetative tissue is created indefinitely after cephalium formation (hypothesis 1; concentric vascular cambium) or stops after several years (hypothesis 2; Mount St Helens). Second, detailed anatomical studies should be carried out to follow the vascular traces going from the primary vascular cylinder to the epidermal juncture between the cephalium and photosynthetic parts, using phloroglucinol (1,3,5-benzenetriol) and hydrochloric acid to follow lignified xylem. It might thus be possible to discern whether there is a bifurcated vascular cambium (hypothesis 1) or merely a dense mass of vascular traces to not yet fully developed axillary buds (hypothesis 2). Third, a cross section through shoot that goes through the sunken margins of the cephalium might reveal whether the vascular traces going from the vascular cylinder to the sunken margins form a complete circle or set of discrete bundles. While this cross-section will not necessarily support or reject the first hypothesis because the hypothesized nascent concentric vascular cambium could have inter-fascicular parts, it would provide additional morphological details.

Conclusion

In some (possibly all) *Discocactus* species, vegetative shoots continue growing after cephalium formation. To do this, *Discocactus* cephalia have a peculiar morphology that has not previously been documented in cacti. Their sunken cephalium appears in radial section as a "W"-shaped border between photosynthetic and reproductive portions of the shoot. Two hypotheses are consistent with these morphological traits: (1) bifurcation of the vascular cylinder resulting in concentric vascular cambia with a circular meristem at the base of the cephalium and (2) heterochronic shifts that cause later development of the photosynthetic portion of the shoot to proceed much more slowly than either early development of the photosynthetic portion of the shoot or development of the reproductive portions of the shoot. Given that heterochronic shifts are far more common than

circular meristems in all plants and concentric vascular cambia have never been documented in cacti, the second hypothesis is *ceteris paribus* more likely, but no data yet exists to test which (if either) hypothesis is correct.

Literature Cited

Buining, A. F. H. 1980. The genus *Discocactus* Pfeiffer: a revision of known, and description of new, species. Succulenta, Nederlands.

Eckardt, N. A. and D. Baum. 2010. The podostemad puzzle: the evolution of unusual morphology in the Podostemaceae. Plant Cell 22:2104.

Gorelick, R. 2013. *Coleocephalocereus purpureus* has a cephalium; *Micranthocereus streckeri* has a pseudocephalium (Cereeae, Cactoideae, Cactaceae). Bradleya 31:142–149.

———. 2014. Axillary branching of lateral cephalia in Cactaceae is not constrained by tilting of shoot apices. Haseltonia 19:13–16.

———. In Press. Strange stem architecture of pachycaulous morning glories. Cactus and Succulent Journal.

——— and M. Machado. 2012. Axillary branching of lateral cephalia of *Coleocephalocereus* (Cactaceae). Haseltonia 17:35–41.

Hernández-Hernández, T., H. M. Hernández, J. A. De-Nova, R. Puente, L. E. Eguiarte, and S. Magallón. 2011. Phylogenetic relationships and evolution of growth form in Cactaceae (Caryophyllales, Eudicotyledoneae). American Journal of Botany 98:44–61.

Mauseth, J. D. 2006. Structure-function relationships in highly modified shoots of Cactaceae. Annals of Botany 98:901–926.

———, T. Terrazas, M. Vázquez-Sánchez, and S. Arias. 2005. Field observations on *Backebergia* and other cacti from Balsas Basin, Mexico. Cactus and Succulent Journal 77:132–143.

Robert, E. M. R., N. Schmitz, I. Boeren, T. Driessens, K. Herremans, J. De Mey, E Van de Casteele, H. Beeckman, and N. Koedam. 2011. Successive cambia: a developmental oddity or an adaptive structure? PLoS ONE 6:e16558, doi:10.1371/journal.pone.0016558.

Rutishauser, R. and K. A. Huber. 1991. The developmental morphology of *Indotristicha ramosissima* (Podostemaceae, Tristichoideae). Plant Systematics and Evolution 178:195–223.

Terrazas, T., S. Aguilar-Rodríguez, and C. T. Ojanguren. 2011. Development of successive cambia, cambial activity, and their relationship to physiological traits in *Ipomoea arborescens* (Convolvulaceae) seedlings. American Journal of Botany 98:765–774.

Vázquez-Sánchez, M., T. Terrazas, and S. Arias. 2005. Morfología y anatomía del cefalio de *Cephalocereus senilis* (Cactaceae). Anales del Jardín Botánico de Madrid 62:153–161.

———. 2007. Morphology and anatomy of the *Cephalocereus columna-trajani* cephalium: why tilting? Plant Systematics and Evolution 265:87–99.